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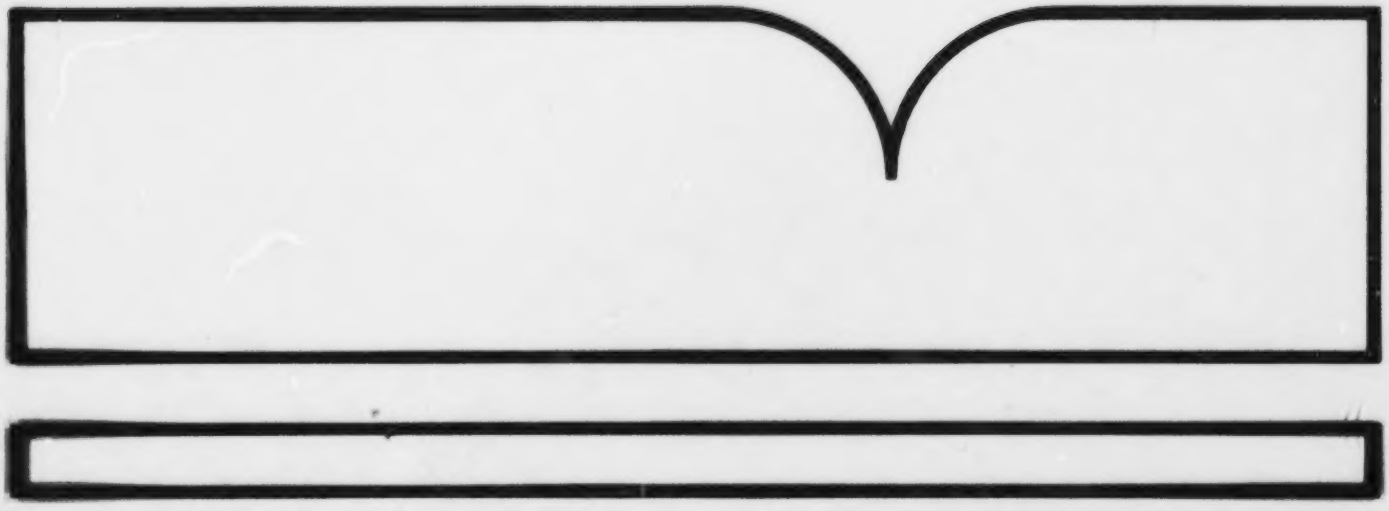

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MICROCOSMS AS ECOSYSTEMS FOR TESTING ECOLOGICAL MODELS

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ABSTRACT

Several microcosm types are currently in use, most to study the fate and effects of toxic substances. An example of the use of microcosms for testing and further development of a model for methoxychlor is described. The finding of an additional dominant process previously unconsidered for methoxychlor is discussed. Three simple ecosystems are considered and compared for their steady state values.

INTRODUCTION

In a pioneering ecological study, Stephen A. Forbes described a lake as forming "a little world within itself--a microcosm ...." In his view of the lake as a microcosm, Forbes saw the system as having clear boundaries, a biota distinct from the surrounding land forms, and physical and chemical processes that act largely independently from the surrounding land. Today, these characteristics remain important to the concept of a microcosm, including its modern usage to denote a laboratory ecosystem rather than a natural water body.

Two additional characteristics -- controllability and observability -- are important also to the use of laboratory

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ecosystems as tools in ecological research. The degree of controllability varies with the philosophy of microcosm operation. If gnotobiotic systems are used and the study organisms are introduced at precisely timed intervals, a rather high degree of control can be exercised. If a naturalistic approach that allows natural associations of microorganisms to colonize is taken, however, the abiotic factors are about all that can be used to influence the system. Microcosms are more readily observable than natural ecosystems because of their small size and because they are usually maintained in the laboratory where data acquisition is convenient.

In every branch of science, a characteristic laboratory approach and associated apparatus have evolved because of their utility and because results obtained by using them are relatable to real world applications of the science. Ecology and environmental science are concerned with the "anatomy and physiology" of the natural world. Consequently, there has arisen a widely held view that only studies that are done in the natural world itself can provide good ecological data. Taken to the limit, this view would inhibit development of ecological theory by inhibiting controlled ecological work. Microcosms can be an effective part of the laboratory approach to ecology. Theories developed either in studies conducted in the natural world or, on the other hand, in the biology or chemistry laboratory can be tested in microcosms. Suitable theory to relate microcosm findings to natural systems, though not currently available, is not inconceivable.

KINDS OF MICROCOSMS

The wide variety of microcosms in use reflects the varied applications for which they have been designed. Generally, a microcosm is used to capture some of the natural-system complexity in a laboratory situation where a degree of control can be exercised. Witherspoon et al. (1976) reviewed the literature on the varied applications of microcosms, including their use in ecological research and in testing the environmental transport of toxic substances. Probably the greatest use that has been made of microcosms is their application to problems of environmental toxicology, the study of the fate and effects of toxic substances in the environment. "The environment," of course, consists of a wide variety of actual environments. Microcosms have been constructed to represent generic classes of environments, or even to simulate particular cases.

Interpretation of the data obtained from studies using microcosms has been the subject of much controversy; critics usually point to factors of real environments not present in microcosms and to the extreme differences of physical scale. In some instances, design criteria have been directed toward permitting a defensible data analysis rationale. Data interpretation and application is, in fact, the major problem associated with the use of microcosms in research. One can clearly see concern with this problem expressed in the wide variety of microcosms that have been constructed. A wide

variety of microcosms has been used for nearly as many special purposes. A few of the more commonly used types are here considered and their uses briefly indicated.

Metcalf microcosms

Perhaps the most widely known microcosm applied today is that developed by Metcalf and coworkers (1971). In this combined terrestrial-aquatic system, the organisms are introduced at carefully staged intervals, the last introduction being mosquitofish (Gambusia affinis). A radiolabeled test chemical is introduced into this system, and samples of water, soil, and the various organisms are analyzed (usually by thin layer chromatography) for their content of parent compound and transformation products after a predetermined time. A biodegradability index is calculated based upon the disappearance of the parent compound, and an ecological magnification index is obtained from the ratio of the concentration in the fish to the concentration in the water. Interpretation of these data and their application is best considered in a relative sense; that is, data from similarly used Metcalf microcosms are comparable. Apparently, no major attempt has been made to develop a rationale for predicting biodegradation or ecological magnification in the environment based upon the indices obtained from these microcosms. It is generally considered, however, that results obtained in Metcalf microcosms are indicative of expected environmental behavior of chemicals.

Multicomponent, transient terrestrial microcosms

Often, concern is expressed about the effect of toxic substances on reproduction of higher organisms in addition to the more direct toxicity effect. A terrestrial microcosm was constructed and operated by Gillette and Gile (1976) for testing such effects on the assumption that effects seen in microcosms will more closely approximate those occurring in nature than would experimentally induced effects by any other method. This rather large microcosm (1 m x 0.75 m x 0.61 m deep) contains a soil mix planted with rye grass, alfalfa, and other legumes. Several invertebrates, a quail (Coturnix coturnix Japonica), a pregnant prairie vole (Microtus canisaudas), and "chameleons" (Anoleus spp) are introduced into the microcosm. Under study conditions, a predetermined quantity of radiolabeled compound is introduced and extensive sampling is carried out to determine the disposition of the compound. This microcosm operates in a transient manner; that is, the animals tunnel and feed upon the above and below ground parts of the growing plants with the result that the vegetation is ultimately decimated. The useful life of these microcosms is established by the rapidity with which this process is completed. Interpretation of data from these microcosms, also, is best made by comparing results of one experiment to another and by considering the results to be indicative of potential environmental effects.

Gnotobiotic microcosms

The use of defined-species (gnotobiotic) microcosms adds an element of control and linkage to results obtained in laboratory studies of the individual species (Taub, 1969; Nixon, 1969). Taub and coworkers have made use of gnotobiotic systems to study the fate and effects of toxic chemicals. In addition to using a single mixed system, physical, open-system compartments have been arranged serially so that organisms of higher trophic levels are maintained downstream of the producer organisms' primary container (Taub, 1969; Morgan, 1972). Mathematical treatment based upon the theory of continuous culture has been used extensively for data interpretation (Taub, 1973).

Excised natural microcosms

In an attempt to overcome the difficulties caused by the undetermined relationship that artificial microcosms have to natural systems, workers at the Oak Ridge National Laboratory have excised small portions of natural terrestrial sites and brought them into the laboratory for further study (O'Neill et al., 1977). These systems each contained a sapling red maple (Acer rubrum) and associated herbaceous ground cover. The excised block of soil was sealed in a wooden container and kept in a greenhouse where the experiment was carried out. These systems were treated with litter from a location downwind of a primary lead smelter. Significantly higher calcium ion concentrations occurred in the leachate from treated

microcosms, and significantly higher CO_2 efflux occurred from their surfaces.

To apply results from such studies to natural systems, it must be possible to use them directly for similar field situations, or to establish that the phenomena are general responses of terrestrial systems to such insults. Attempts were made in this study to observe related phenomena in the field for validation. In the field study, the size of the magnesium pool immobilized in litter was found to be larger where the pollutant (lead) was higher, and this observation was interpreted to indicate disturbances in nutrient cycling.

Scaled process microcosms

Frequently, it is asked how well a microcosm represents a natural environment. Usually there is no basis on which to attempt to answer such a question, although attempts have been made to scale processes in microcosms to match those in the natural system that they represent. Perez et al. (1977), for example, attempted to scale light, benthic surface to water volume ratio, water turnover time, and turbulence to observed conditions of Narragansett Bay. Algae responded to the microcosm experiments by growing to higher levels than in the natural system. Their tentative conclusion was that turbulence was a major controlling influence in the systems.

Cooper and Copeland (1973) used scaled, open-system microcosms in series to represent the exchange and retention properties of Trinity Bay, Texas. The systems were used to

consider the influence of variations in input rates of water and Kraft mill effluents. Lower input rates of water resulted in lowered productivity and respiration rates. Inputs of Kraft mill wastes resulted in large responses in upstream cells in which primary productivity decreased and respiration increased. To relate to the environment it was assumed that results obtained in the microcosms directly represented expected results in Trinity Bay for the environmental conditions studied.

Vogel and LaBarbera (1978) discussed the potential uses of flow tanks for biological research and teaching. They presented useful descriptions for means of calculating and measuring to simulate and scale properties of real, flowing systems.

Scaled properly, microcosms can be considered to be legitimate surrogates for specific natural systems. The scaling process provides the scale factors for application of results to the real world.

Microcosms for selected biological associations

In a unique approach to microcosm work continuous culture techniques were used with toxic chemicals as the carbon substrate to isolate functional biological associations (Senior et al., 1976). In these associations the organisms present are related to others in a symbiotic way. In the classical theory of continuous culture, competition among several organisms for growth-limiting nutrients reduces the community to a single

surviving population. In this case, however, when the community was selected four primary utilizers of the limiting substrate, Dalapon, existed through several, long-term experiments over a wide range of dilution rates. Apparently some unidentified interactions occurred among the primary utilizers or with other organisms present to stabilize the community. Studies with microcosms of this sort (chemostats) show promise of elucidating biological mechanisms whereby xenobiotic compounds are decomposed.

Perhaps more importantly elucidation of the operative mechanisms stabilizing a multispecies association of decomposers in a chemostat could provide significant contributions to our knowledge of competition within an ecological functional group. Current mathematical theories usually predict a single surviving species, unless true competition does not exist.

Microcosms with separated, major, ecological functions

After concluding that unbalanced mineral cycling is characteristic of most aquatic microcosms, Ringelberg and Kersting (1978) constructed a well conceived system designed to overcome this difficulty. In their system they used three separate but connected containers for enhancing primary productivity, herbivory, and decomposition. The autotroph and herbivore units were illuminated in a day-night cycle, the herbivorous unit being kept at significantly lower intensities than the autotrophic unit. The decomposer unit was kept in

complete darkness. In the large system (two sizes were used) steady states were achieved in the autotrophic unit, and in the small system the pattern of the whole system was "consistent." For the large system an operating time of at least 100 days was required before it could be confidently concluded that a steady state existed after an event (such as change in flow rate) had induced a transient.

The work with these microcosms was done primarily to try to achieve functioning, long-lived micro-ecosystems for use as an experimental tool in ecological studies. The results reported indicate that significant progress has been made toward this goal. Ringelberg (1976), in discussing the possibilities for this microcosm, advocated its use particularly in studies of toxic substances. Kersting (1975) used replicate small systems for such studies.

Naturally derived, self developed microcosms

Rather than try to scale or mimic any real, natural ecosystem we have taken a different approach at our laboratory. We view every natural ecosystem as a unique, and therefore non-duplicable, combination of physical, chemical, and biological components. In our view, studies of ecosystems, therefore, must focus upon functional similarities. Application of the results of one field study to another field situation is generally made by relating the functions studied using system (intensive and extensive) properties common to both systems. We view microcosms as ecosystems (as contrasted

to imitators of ecosystems), and thus microcosm results can be related to field situations by the same process whereby one field study is related to another. Identification and elucidation of the relationships whereby extropolation can be made is the major challenge to microcosm experimentalists and theorists.

In studying the fate of toxic substances, we consider each of the separate processes that remove the chemical from the system (Baughman and Lassiter, 1977), including physical removal (such as volatilization), chemical removal (such as hydrolysis), and biological decomposition. These processes are functions of the environment, and with the exception of biological decomposition, are well understood. To represent these physical and chemical processes, we have only to measure the environmental parameter to use in the process description. For biological processes, however, the task is somewhat more complex. We have postulated that open systems into which a wide variety of biological forms are continually introduced will reach a functional steady state that will be identical for all systems whose abiotic components are identical. This is essentially the same idea as that expressed by the climax community of ecology. It has application for our microcosms, however, because we establish the biological communities in exactly that way; that is, by continual introduction of a wide variety of organisms into replicate laboratory microcosms (Brockway et al., 1978). That one of the functions will be the

capability of the system to degrade the chemical at a characteristic rate remains conjectural and should be checked for a variety of systems. One such system was studied for the insecticide, methoxychlor.

Fate of Methoxychlor in a Naturally Derived, Self Developed Open Microcosm. Methoxychlor, a chlorinated hydrocarbon insecticide that is often used as a substitute for DDT (Morley, 1977), was selected for use in a recent joint modeling and microcosm experiment (Brockway et al., 1978) at our laboratory. The objective was to use the model to predict the fate (concentrations in water, biomass, and sediment) of methoxychlor and to test whether the model was capable of predicting the fate of methoxychlor in the simple laboratory ecosystem. Model predictions were based upon sorption to biomass and sediment, and assumed biodegradation by small microbial populations. Literature sources indicated low microbial degradation rates. Walker (1978) reported losses ranging from 5 to 8 percent after 84 days of incubation. Paris and coworkers (1975) were able to find only one population (Flavobacterium harrisonii) that degraded methoxychlor. In view of these results, low reported chemical degradation (hydrolysis) and direct photolysis rates (Wolfe et al., 1976), the absence of reported high environmental concentrations was puzzling. Only sensitized photolysis from southeastern U.S. waters with high humic acid levels (Wolfe et al., 1976) is reported to occur at significant rates. Kapoor and coworkers

(1970) reported that higher organisms metabolize methoxychlor to water soluble compounds, but this pathway is not likely to be a significant sink from the environment because of the relatively small higher organism biomass. And, of course, there were no higher organisms in our microcosms.

Based upon these considerations a low rate of methoxychlor decomposition was predicted. However, a rapid disappearance of methoxychlor occurred in the experiments. Followup experiments were carried out using measured quantities of organisms from the microcosms to determine what was responsible for the degradation. Tests were run in light and dark using live organisms, killed organisms, and filtered microcosm water. The only systems showing rapid degradation were those with live organisms in the light. A typical curve for the concentration of methoxychlor with time in the experiments with light and organisms is given in Fig. 1.

Preliminary analysis of biological decomposition of methoxychlor in light. The process was postulated to be second order:

$$\frac{dC_T}{dt} = -kC_W b \qquad (1)$$

where C_T is total concentration of methoxychlor in the system,

C_W is concentration of dissolved methoxychlor,

b is concentration of biomass, and

κ is the second order rate coefficient.

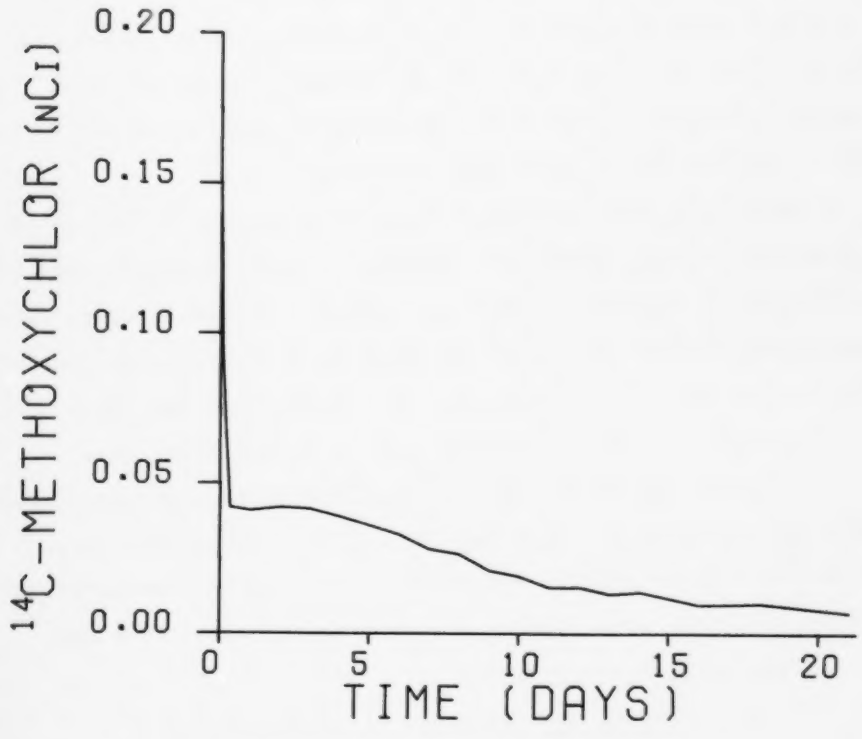


Figure 1. Concentration of methoxychlor in solution with time during an experiment with algal community under 12-hour light dark cycle. Rapid initial decrease is sorption, slower decrease is decomposition buffered by simultaneous desorption.

Methoxychlor partitions rapidly to solids. (Note the rapid initial drop of water concentration in Fig. 1.) Therefore, equilibrium partitioning was assumed:

$$\frac{C_S}{C_W} = K_p \tag{2}$$

$$C_T = C_S b + C_W \tag{3}$$

where K_p is the solid-water partition coefficient, and

C_S is the concentration of methoxychlor per unit of biomass.

At the end of the experiment, an overall K_p obtained for the experimental units on the basis of dry weight of the biomass (mostly algal) was about 1.8×10^4.

From the two equations above,

$$C_W = \frac{C_T}{1 + K_p b} \tag{4}$$

Thus, the equation for methoxychlor disappearance becomes

$$\frac{dC_T}{dt} = \frac{-kC_T b}{1 + K_p b} \tag{5}$$

For each experiment, biomass was fixed at one of three levels: 0.1, 1, or 3 g/500ml (blotted wet weight, about 9 times the dry weight). It was assumed (at least to a first approximation) that biomass remained constant throughout the course of the experiment. The factor $kb/(1 + K_p b)$ is, therefore, constant, with the result that the integrated equation is simply

$$C_T = C_{TO} \exp\left(\frac{-kbt}{1 + K_p b}\right) \tag{6}$$

Substituting again to obtain an expression for C_W, because the measurements were made on C_W,

$$C_W = C_{WO} \exp \frac{-kbt}{1 + K_p b} \tag{7}$$

The apparent rate coefficient was obtained by fitting regression of log C_W versus t for each experiment. The slope of this fit is the apparent rate coefficient:

$$\frac{kb}{1 + K_p b} \tag{8}$$

Thus, the second order rate coefficient is obtained by multiplying by $1 + K_p b$ and dividing by b, the biomass for the experiment. The resulting value was $(2.7 \pm 0.2) \times 10^{-4}$ L mg algae^{-1} hr^{-1}. The low standard error of the estimate apparently confirms that the transformation process is indeed second order in biomass and methoxychlor. The functional relationship of this process to light intensity remains to be determined.

Microcosms as experimental ecosystems for testing models. The microcosm, or experimental ecosystem, experiment was carried out to test whether laboratory data are useful in predicting the fate of chemicals in ecosystems. A similar kind of test was carried out for chlorpyrifos by Neely and Blau (1977) for small, experimental-fish-pond ecosystems. Their conclusions were that the simple laboratory measurements can be used to predict real world results with a high degree of credibility. In our attempt to do this using methoxychlor in the laboratory

ecosystems, an apparent contradiction of the simple laboratory data was noted. Follow up experiments, however, showed that another previously unidentified process, decomposition by the algal community in the light, accounted for the discrepancy. This finding illustrates the utility of testing models of the fate of toxics in experimental ecosystems. In a mathematical model representation, only suspected processes are accounted for. In experimental ecosystems in contrast to natural systems, we control abiotic factors and can therefore discount them as causes of differences between model and experiment. The mismatch between the microcosm results and the model predictions is, therefore, indicative that a process is poorly described or missing. The value of using microcosms as experimental ecosystems is also seen when specific model hypotheses require special characteristics of ecosystems for a critical test to be performed. Microcosms can be controlled over a wide range to include much of the variety of characteristics necessary for critical tests of models.

FUTURE DIRECTIONS IN MICROCOSM RESEARCH

Much of the microcosm work of the past has been done on an ad hoc basis. It will undoubtedly continue to be desirable to design and use microcosms on an immediate-need basis. Where microcosms are needed as models or facsimiles of natural systems it is appropriate that they be built for the specific need at hand (Neuhold and Ruggerio, 1976). The solution to a pressing problem is usually most efficiently done by tailoring

the solution technique specifically to that problem. Furthermore, many good ideas that are widely applied have arisen as ingenious solutions to specific problems. It is not desirable, however, to pursue ad hoc microcosms to the exclusion of more general questions.

Microcosms are a special class of ecosystems because of their extensive properties. Those properties are related to size (transport, migration distances, magnitudes of gradients, etc.), but imaginative design can overcome many of the limitations of microcosms associated with their small size (e.g., the system of Ringelberg and Kersting, 1978). With respect to intensive properties (concentrations, population interactions, rate constants, etc.) microcosms can represent nearly as wide a variety of situations as those that occur in the natural world. Ecological theory and the ecologically related literature, in general, suffer from a failure to distinguish between intensive and extensive properties. The ecological literature is replete with reports of "differences" in net rates between systems of different extent. It would be worthy of note if a similarity between natural systems were found, but differences are hardly noteworthy - they are expected. Even more common is the uncritical reporting of net rates (uptake, decomposition, etc.) without indicating the size (or unit activity) of populations involved. Nature is undoubtedly parsimonious and harmonious, but to what extent this is so is not clear because the underlying relationships

that depend upon intensive properties frequently have not been separated from the extensive properties of natural systems as distinctly as they have been in physics and chemistry.

There are, of course, interactions between intensive and extensive properties of systems, particularly ecosystems. Virtually all ecosystems are open systems. Whereas in closed systems the equilibrium state is a function of the initial state, in open systems the steady state is a function of its imput and output and is completely independent of the initial state. Von Bertalanffy (1950) has discussed the idea of equifinality in chemical and biological systems. Here systems with equivalent input, output, and physical characteristics reach equifinal states regardless of their initial states. Whittaker (1955) considers the climax community to be an example of this equifinal steady state. It is not clear, however, what the exact interpretation of this result should mean for ecosystems in general. That is, it is not clear whether identical species structures are expected as the steady state for abiotically identical communities, or whether functional identity of steady states can be reached without species identity. This is a theoretical question that can be investigated experimentally only by the use of microcosms (because true replication is required), and for which especially careful formulation of hypotheses is necessary to avoid becoming enmeshed in tautology. Whatever the outcome of such an experiment to interpret the meaning of ecological

equifinality, it appears safe to assume that in one sense or the other, von Bertalanffy's concept of open system equifinality is as true of ecosystems as it is for abiotic systems.

System configuration and input-output characteristics, however, are extensive properties of systems. For ecosystems these properties select the quantity and type of biota that exist in the system, and therefore establish whether certain functions (characterized by intensive properties) exist in the system. As examples, the number of trophic levels depends in part upon the size of the system and the input-output characteristics of O_2 in part establish whether anaerobiosis occurs.

A theoretical basis exists for the analysis of open system microcosms within the literature on continuous culture of microorganisms. Herbert and coworkers (1956) discussed rather completely the theory of continuous culture of microorganisms in single-stage open systems, and Herbert (1962) and Fencl (1966) extended the theory significantly to include multistage systems (open systems connected in series). Williams (1971) presented some theory of algal growth in chemostats. Bailey and Ollis (1977) considered additional trophic levels.

In using open-system microcosms, a higher degree of complexity than is generally the case in chemostats will be desirable, although Tsuchiya et al. (1972) and Canale et al. (1973) considered complex system structures in chemostats. The

equifinality result applies to systems whose internal structure remains the same. Where different structures are possible, interactions within the systems influence the form of the steady state. Thus, any mathematical modeling or analysis of complex microcosms must depend upon some knowledge of the system structure. It is of interest to compare the expressions for the steady states of hypothetical systems of different complexities for differences in their functional dependencies.

In these systems, the functional components are considered to be a nutrient resource (N) that flows in from the outside and is utilized by a producer (P). In most chemostat theory, the resource is assumed to be an organic substance and the utilizer organism, a heterotrophic microorganism. With the choice here of a primary producer for the simplest system, addition of system functional components can proceed naturally in constructing the more complex systems. In these systems nonliving, organic material (O) is assumed to derive from the living organisms. A decomposer (D) that mineralizes the organic, returning it to the inorganic form, is further assumed to exist. Finally, in the most complex system considered, a grazing consumer (Z) is assumed to feed upon P. These components are represented as having fixed birth and death rate constants. This assumption probably means that each system component is legitimately considered to be representative of a single species population. Whether it is legitimate to represent a whole functional complement of species by such

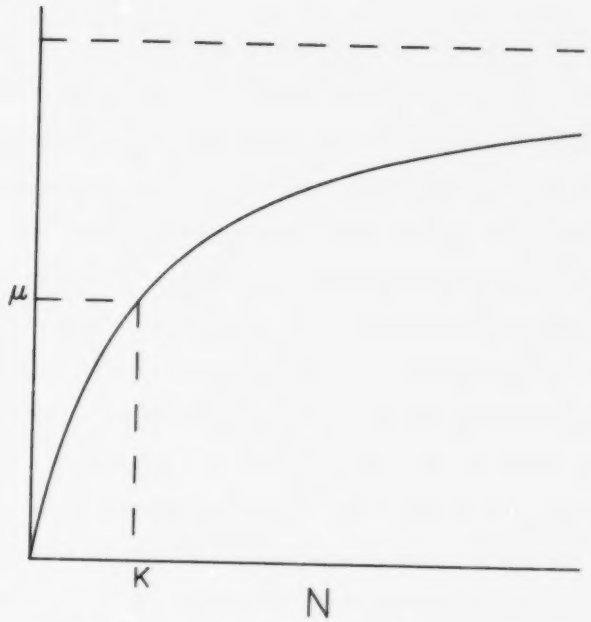
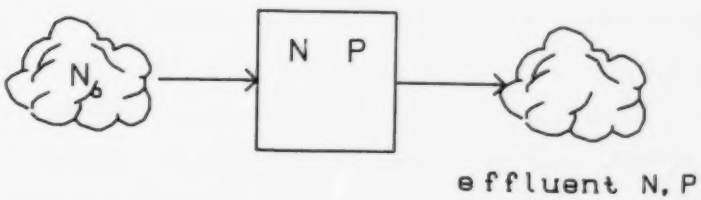


Figure 2. Form of relationship between growth rate constant, μ, and substrate, N, used in the simple community models. Algebraic form is the well known, rate limited growth expression of Monod.



SYSTEM 1 = CHEMOSTAT

Figure 3. System 1 is a chemostat representation. Only one kind of organisms, assumed to be photoautotrophic users of the single substrate, N, exist in the system. Photoautotrophs are assumed merely for continuity with Systems 2 and 3.

equations is not clear. In any case, the models are assumed to be reasonable simplifications so that interactions among the system functional components can be made clear. For all living components, rate-limited growth (Fig. 2) is assumed.

System 1, the chemostat

The chemostat, Fig. 3, is described by the following equations:

$$\frac{dP}{dt} = \left[\hat{\mu}\left(\frac{N}{K+N}\right) - d_p - \frac{1}{\theta}\right] P \tag{9}$$

$$\frac{dN}{dt} = -\frac{\hat{\mu}}{Y}\left(\frac{NP}{K+N}\right) + \frac{N_o - N}{\theta} \tag{10}$$

where

$\hat{\mu}$ is max growth rate
K is half saturation constant
Y is yield coefficient
θ is retention time (vol./flow)

Term descriptions are

$\frac{dP}{dt}$ = growth (N P) - death - outflow

$\frac{dN}{dt}$ = - growth (N P) + inflow - outflow

The steady state solutions are

$$\breve{N} = \frac{K(1 - d_p\theta)}{\hat{\mu}\theta - (1 + d_p\theta)} \tag{11}$$

$$\breve{P} = \frac{Y(N_o - \breve{N})}{1 + d_p\theta} \tag{12}$$

$$= Y\left(\frac{N_o}{1 + d_p\theta} - \frac{K}{\hat{\mu}\theta - (1 + d_p\theta)}\right)$$

If d_P is negligibly small:

$$\breve{N} = \frac{K}{\hat{\mu}\theta - 1} \tag{13}$$

$$\breve{P} = Y\,(N_o - \breve{N}) \tag{14}$$

$$= Y\left(N_o - \frac{K}{\hat{\mu}\theta - 1}\right)$$

Note that the steady state nutrient concentration, $\breve{N}$, is independent of its input concentration, N_o, but that $\breve{P}$ is a function of N_o. Not only is $\breve{N}$ independent of N_o, it is also independent of $\breve{P}$, being a function only of the physiological parameters of P and retention time, θ. Note also that both (and for that matter all the succeeding steady state results) display the open-system property of independence of their initial state.

System 2, recycling

The relationships among the system components are shown in Fig. 4. The describing equations are

$$\frac{dP}{dt} = \left[\hat{\mu}_P \frac{N}{K_{NP} + N} - d_P - \frac{1}{\theta}\right] P \tag{15}$$

$$\frac{dN}{dt} = -\hat{\mu}_P \left(\frac{NP}{K_{NP} + N}\right) + \left(\frac{1}{Y} - 1\right) \hat{\mu}_D \left(\frac{O}{K_O + O}\right) D + \frac{N_o - N}{\theta} \tag{16}$$

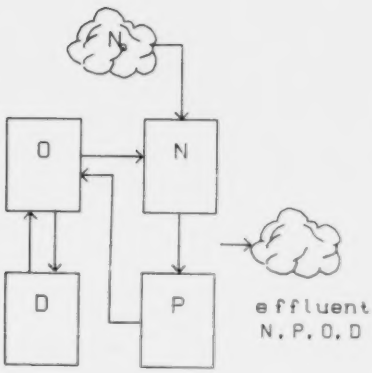


Figure 4. System 2 with internal recycling consists of producers (P, photoautotrophs) using substrate, N, producing organic material, O, which is remineralized by decomposers, D, to the substrate.

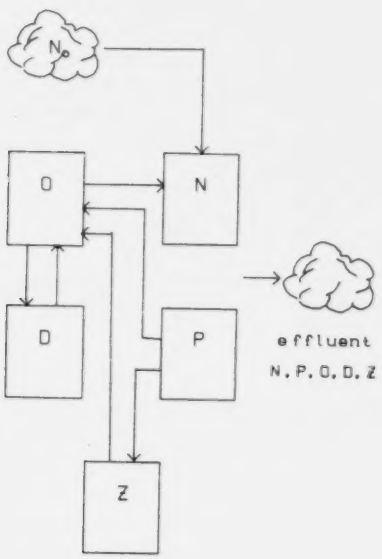


Figure 5. System 3 is System 2 plus a consumer, Z, utilizing producers as substrate and producing organic material.

$$\frac{dD}{dt} = \left[\hat{\mu}_D \left(\frac{O}{K_o + O}\right) - d_D - \frac{1}{\theta}\right] D \tag{17}$$

$$\frac{dO}{dt} = d_P P + d_D D - \frac{\hat{\mu}}{Y} \left(\frac{O}{K_o + O}\right) D - \frac{O}{\theta} \tag{18}$$

Term descriptions are

$\frac{dp}{dt}$ = P growth - P death - P outflow

$\frac{dN}{dt}$ = -P growth + D mineralization + N inflow - N outflow

$\frac{dD}{dt}$ = D growth - D death - D outflow

$\frac{dO}{dt}$ = P death + D death - D (growth + mineralization) - O outflow

The steady state solutions are

$$\breve{N} = \frac{K_{NP} (1 + d_P\theta)}{\hat{\mu}_P\theta - (1 + d_P\theta)} \tag{19}$$

$$\breve{O} = \frac{K_o (1 + d_D\theta)}{\hat{\mu}_D\theta - (1 + d_D\theta)} \tag{20}$$

$$\breve{D} = \frac{\breve{O} - (N_o - \breve{N}) \left(\frac{d_P\theta}{1 + d_P\theta}\right)}{\left(\frac{1}{Y} - 1\right)\left(\frac{d_P\theta}{1 + d_P\theta}\right)(1 + d_D\theta) - \frac{(1 + d_D\theta)}{Y} + d_D\theta} \tag{21}$$

$$\breve{P} = \left(\frac{1}{Y} - 1\right) \frac{(1 + d_D\theta)}{(1 + d_P\theta)} \breve{D} + \frac{(N_o - \breve{N})}{(1 + d_P\theta)} \tag{22}$$

In this system, the increased complexity of the internal relationships has resulted in a much more complex expression for the steady state level of producer, $\breve{P}$. It is not entirely

controlled by, but is still a function of, N_o. In contradistinction, the steady state nutrient concentration is completely unaffected by the additional complexity of the system. Its form is identical to that in system 1. In a similar way the steady state concentration of organics, $\breve{O}$, depends only upon the physiological parameters of D and retention time, θ.

System 3, food chain

The form of interactions assumed when grazers, Z, are added are shown in Fig. 5. This system is described by the following equations.

$$\frac{dP}{dt} = \left[\hat{\mu}_P \left(\frac{N}{K_{NP} + N} \right) - d_P - \frac{1}{\theta} - \frac{\hat{\mu}_Z}{Y_{PZ}} \frac{Z}{(K_{PZ} + P)} \right] P \qquad (23)$$

$$\frac{dN}{dt} = - \hat{\mu}_P \left(\frac{NP}{K_{NP} + N} \right) + \left(\frac{1}{Y_{ND}} - 1 \right) \hat{\mu}_D \left(\frac{O}{K_O + O} \right) D + \frac{N_o - N}{\theta} \qquad (24)$$

$$\frac{dD}{dt} = \left[\hat{\mu}_D \left(\frac{O}{K_O + O} \right) - d_D - \frac{1}{\theta} \right] D \qquad (25)$$

$$\frac{dO}{dt} = d_P P + d_D D + d_Z Z - \frac{\hat{\mu}}{Y_{ND}} \left(\frac{O}{K_O + O} \right) D + \left(\frac{1}{Y_{PZ}} - 1 \right) \hat{\mu}_Z \left(\frac{PZ}{K_{PZ} + P} \right) - \frac{O}{\theta} \qquad (26)$$

$$\frac{dZ}{dt} = \left[\hat{\mu}_Z \left(\frac{P}{K_{PZ} + P} \right) - d_Z - \frac{1}{\theta} \right] Z \qquad (27)$$

Term descriptions are

$$\frac{dP}{dt} = \text{P growth - P death - P outflow - Z grazing}$$

$$\frac{dN}{dt} = \text{-P growth + D mineralization + N inflow - N outflow}$$

$$\frac{dD}{dt} = \text{D growth - D death - D outflow}$$

$$\frac{dO}{dt} = \text{P death + D death + Z death - D (growth + miner.) + Z excretion - O outflow}$$

$$\frac{dZ}{dt} = \text{Z growth - Z death - Z outflow}$$

Steady state solutions are

$$\breve{P} = \frac{K_{PZ}\,(1 + d_Z\theta)}{\hat{\mu}_Z\,\theta - (1 + d_Z\theta)} \tag{28}$$

$$\breve{O} = \frac{K_O\,(1 + d_D\theta)}{\hat{\mu}_D\,\theta - (1 + d_D\theta)} \tag{29}$$

$$\breve{Z} = \frac{Y_{PZ}\,\breve{P}\left[\breve{\mu}_P\,\theta - (1 + d_P\theta)\right]}{\breve{\mu}_Z\theta}\,,\quad \breve{\mu}_P = \frac{\hat{\mu}_P\,\breve{N}}{K_{NP} + \breve{N}}\,,\quad \breve{\mu}_Z = \frac{\hat{\mu}_Z\,\breve{P}}{K_{PZ} + \breve{P}} \tag{30}$$

$$\breve{D} = \frac{\breve{\mu}_P\,\breve{P}\breve{O} + \breve{N} - N_o}{\left(\frac{1}{Y_{ND}} - 1\right)(1 + d_D\theta)} \tag{31}$$

$$f(\breve{N}) = d_P\breve{P} + \left(\frac{1}{1 - Y_{ND}}\right)\left(\frac{d_D\,Y_{ND}\theta}{1 + d_D\theta} - 1\right)\left(\breve{\mu}_P\breve{P} - \frac{(N_o - \breve{N})}{\theta}\right) \tag{32}$$

$$+ \left[d_Z + \left(\frac{1 + d_Z\theta}{\theta}\right)\left(\frac{1}{Y_{PZ}} - 1\right)\right]\left[\frac{Y_{PZ}\,\breve{P}}{\breve{\mu}_Z}\right]\left[\breve{\mu}_P - \left(\frac{1 + d_P\theta}{\theta}\right)\right] - \frac{\breve{O}}{\theta}$$

The introduction of grazers makes a major difference in the functional dependencies of the system components. $\breve{N}$, formerly dependent upon the parameters of P and retention time, here is a rather complicated implicit function dependent upon its own

supply rate. With grazers present, the steady state level of producers is independent of N_o and $\breve{N}$; therefore, $\breve{N}$ is no longer a function of the parameters of P.

The results can be taken to indicate steady state relationships in ecosystems coupled in the ways indicated, but because these equations represent biological systems, much more complexity should be expected than is apparent here. In system 3, for example, $\breve{P}$ and $\breve{O}$ are functions of parameters of other system components and residence time, whereas $\breve{Z}$, $\breve{D}$, and $\breve{N}$ are functions of N_o, physiological parameters, and residence time. In a real-world open system, Z and D are selected during ecological succession largely by action of the extensive properties, N_o and θ. Their physiological parameters, because of the selection, are functions of N_o and θ, thereby making $\breve{P}$ and $\breve{O}$ functions of N_o and θ.

These equations can represent only microcosm ecosystems because complete mixing and constant inflow and outflow are assumed. Only in microcosms can such assumptions be closely approximated. The equations, however, preserve much of what is considered important and characteristic of ecosystems, without containing superfluous detail. It should be possible to use equations of this simplicity to explore hypothetical ecological hypotheses and to use microcosms to test them. By varying the extensive properties of the systems, N_o and θ, one could design the microcosms to test the hypotheses. Even in this superficial treatment, it appears that systems from which

consumers are excluded behave in one way, whereas the presence of consumers switches the system to entirely different steady state dependencies. This hypothesis needs to be confirmed or refuted.

One of the important, but presently impossible to fulfill, needs is the capability to predict ecological effects of toxic substances. Although much of the current use of microcosms is involved in research on this general need, it is not apparent that any general approach to the problem is being made. Although the term "ecological effects" is common, most studies are directed toward effects on individual organisms. Perhaps less obvious effects on system function should be as great a concern. Without a better ecological theory to comprehend what is the normal behavior of unaffected ecosystems, there is little basis for establishing affected behavior. A theory of open-system microcosms will provide a basis for research on such questions. A general theory of open-system microcosms extending the results of continuous culture theory should be developed. Such a theory would enhance general ecological theory as well.

CONCLUSIONS

Although microcosms have been widely used and are currently being used in studies for toxic chemicals, there is little or no quantitative theory to use for relating microcosm results to the real world. Microcosms have been used successfully to test a model of the fate of a toxic chemical. They are useful for

such tests because the control over environmental factors permits discrepancies between predicted and observed to be interpreted as a model fallacy rather than as results of unknown fluctuations in the environment. A significant feature of ecosystems is that they are open systems. Open system microcosms exhibit general characteristics of ecosystems and a quantitative theory should be developed for open microcosms. Many aspects of this theory would be applicable to natural ecosystems. It would be useful in relating results obtained in open microcosms to natural ecosystems.

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